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Patterns of Distribution of Paspalum species along environmental gradients landscapes in the Nicaraguan Dry Tropical Forest

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Preface

This master thesis is written as a part of the project Multi-functional – Landscapes financed by the Research Council of Norway (2009-2012) and led by Graciela Rusch at the Norwegian institute for Nature Research.

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Abstract

The influence of different environmental conditions over the distribution patterns of four *Paspalum* species, and their physiological performances was assessed at different scales. A set of transects were laid out across the silvopastoral landscapes in three regions of the Nicaraguan Dry Tropical Forest. In these transects, 20 x 20 m² plots were located and the variables: soil types, topography, vegetation structures and land covers were recorded. Inside these plots a 20 m line was traced and the basal cover of the *Paspalum* and their chlorophyll fluorescence values were measured. The non *Paspalum* species were listed at 20 x 20 m² plot and 20m line. At regional scale the land use dynamic seems to be the factor driving the patterns of distribution of the *Paspalum* species. Introduction of exotic grasses, agriculture extension and the constant rotation of agriculture and livestock farming seems to affect negatively the presence of these *Paspalum* species in Rivas. The four target species were present in Muy Muy, where the agriculture is less intensive and the introduction of sown pasture is less extended. At local scale soil and altitude seemed to be the factors limiting the distribution of the species. *Paspalum conjugatum* tended to occur at high altitudes in sloping places surrounded by forested ecosystems at soils with neutral pH. It was capable to form patches but not a continuous grass carpet. *Paspalum notatum* tended to occur in acid soils, avoiding neutral soils and the highest altitudes. It is the most extended target species across the landscapes. It is able to form extended grass carpets. *P. centrale* is a generalist occurring scattered with lower abundances avoiding sites with neutral soil pH. *Paspalum virgatum* occurred scattered with lower abundances in a wide variety of conditions and land uses, which was interpreted as a generalist behavior capable to thrive even in disturbed conditions. The positive correlations between the basal cover of all the species and their fluorescence values can be interpreted as a good indicator that the abundance of the specimens reflects high physiological performance

Patterns of Distribution of *Paspalum* species along environmental gradients landscapes in the Nicaraguan Dry Tropical Forest

With about 330 species (Denham et al. 2010), *Paspalum* L. is one of the largest genera within the *Poaceae* family (grass family). The majority of the species is native of the Neotropics and occurs in a diversity of ecological conditions across North, Central, and South America. The centers of highest taxonomic diversity are in the Brazilian Cerrados and the Campos of Argentina, Uruguay, and southern Brazil. A few species are found in Africa, Asia, and Oceania, three or four can be regarded as pan-tropical and one species occurs in the Antarctica (Clayton et al. 2012), but the genus is thought to have originated in tropical South America (Chase 1929). *Paspalum* are an important component of the biodiversity of herbaceous vegetation in the neotropics (Rua et al. 2010). One species, *Paspalum scrobiculatum* L. is cultivated as a cereal in Asia and some species like *Paspalum notatum* Fluggé and *Paspalum dilatatum* Poir., are regarded as a valuable forage grasses (Filgueiras 1992, cited by Rua et al. 2010).

The species of *Paspalum* often dominate open areas, but some species can occur in forests and environments with tree cover, coastal dunes and halophytic (with high content of salt) habitats. Many species have a weed behavior, occurring along roadsides, railroads and disturbed soils (Denham et al. 2010). *Paspalum* have both sexual and apomictic modes of reproduction (Hojsgaard et al. 2009). Due to its asexual reproduction and the capacity for rapid spread, *P. conjugatum* and *P. notatum* are considered a threat for some important crops in Mesoamerica as agave,

rice, oat, peanut, coffee, sugar cane, fruit trees, corn and plantain crops (Villaseñor et al. 1995, Acosta & Agüero 2002).

Grassland ecosystems in Central and South America are severely threatened by the expansion of agriculture and the replacement by exotic forage species (Rua et al. 2010). Despite the richness of Neotropical grass species, the large majority of grass forage species cultivated throughout the tropics are originally from Africa, where they evolved together with large grazers. The selection pressure has led to more productive, vigorous, robust and grazing tolerant species than those American species (*Paspalum* spp. and *Axonopus* spp.) evolved under lower grazing pressure from smaller animals (Jank et al. 2011). At least six species of African grasses (*Panicum maximum* Jacq., *Brachiaria mutica* (Forsk.) Stapf, *Melinis minutiflora* Beauv., *Hyparrhenia rufa* (Nees) Stapf, *Pennisetum clandestinum* Hochst., and *Digitaria decumbens* Stent) have been involved in massive ecological invasions, often become naturalized and spread rapidly and widely (Parsons 1972). However, more studies from cultivated grasslands are necessary in order to clarify which exotic grass species are really present in Central America.

In Central America, savannas and grasslands are often replaced by pastures sown with exotic grasses to increase the amount and quality of the food for cattle (Dias-Filho 2007, cited by Ospina 2010). However, Ospina et al. (2012) demonstrated in the area where this study was conducted, that the sown pastures are more productive than grasslands in the wet season but the productivity of grasslands is more stable along the year and less dependent on the rainy season. Furthermore, sown pastures and grasslands did not differ in total yearly above ground productivity. The

introduction of standard and homogeneous crops may boost productivity, particularly when the introduction of cultivars is accompanied by the addition of resources (irrigation, fertilization), but leads to the loss of innumerable heterogeneous and often locally adapted varieties (Esquinas-Alcazar 2005, cyted by Balmford 2008). This lost results in irreversible loss of the genetic diversity, known as genetic erosion (Balmford 2008).

Some species of *Paspalum* have been favored for research programs due to its economic importance and information about ecology, uses and management is available for those species. The taxonomy is more or less well known including some information about the phylogeny of the genus (Denham et al. 2010, Rua et al. 2010). However, living collections and data on genetics and reproduction for more species are far scarce. The evolution of the genus is not documented (Rua et al. 2010).

The taxonomy of the Nicaraguan grasses is well known. Davidse and Poll (W3Tropicos 2012) report 44 *Paspalum* species in the country and four more are expected as they occur in nearby countries. However, transmission of this taxonomical knowledge to the users is limited and the local capability of grasses identification is often low

The knowledge about life-history, ecological, taxonomical and evolutionary characteristics of these species varies. Those with economic importance have received more attention, but the information available decreases with decreasing economic importance of the species.

Balmford (2008) propose three steps to quantify and map the global diversity of crops and livestock, and how it might change. 1) To map the distribution of wild relatives and of local varieties and breeds. 2) To obtain

an estimate of the economic value of each breed variety as insurance against pest and disease outbreaks. 3) The comparison between states of the world would allow for an estimate of which breeds/varieties would be more likely to be loss given their spatial distributions. This study will make a contribution to the first step, by understanding the factors underlying the distribution of native varieties of forage grasses and some of its wild relatives in Nicaraguan Dry Tropical Forest. The conservation of animal and plant resources for food and agriculture relies on the preservation of both, the variety of domesticated species and their wild relatives (Balmford 2008). The *in-situ* conservation is considered as one of the principal obligations for the conservation of biological diversity (W3CBD 2011). Further, to know the physical and biophysical environment of the managed landscapes and its influence on the distribution of these target species could help to improve its *in-situ* conservation in Central America. At least four native species of the grass genus *Paspalum* are frequent in grasslands of the dry tropical forest of Nicaragua. These species could have a potential for development as locally adapted forage plants. Thus it is important to understand how these species are affected by the current land use, which ones co-exist, the extent to which they occupy different habitats, and have different abiotic requirements. This knowledge helps to improve the use and management of the forage species and avoid depletion of the local diversity by the introduction of few exotic species when production and economic benefits are not sufficient to justify the change. By knowing the requirements of the different native species it is possible to attempt a temporal and spatial zoning of improved pastures with locally adapted forage plants. Further, knowledge about within population diversity, which is indicative of specific adaptations to the

physical environment and to interactions with other organisms (i.e. large herbivores, trees and insects), will help to better value genetic diversity of important forage species.

Objective

The overall objective is to assess which are the main land-use and abiotic factors that are related with the distribution patterns of native grass species. Specifically, the following questions are addressed:

1. The factors affecting the regional patterns of distribution.
2. The factors affecting distribution and abundance within areas (topographic position, altitude, habitat type and soil, etc)
3. The differences in abundance and distribution among the four species
4. The relationship between the local abundance of the species and their physiological performance.

Methods

Study species

Four native grass species of the genus *Paspalum* that are potentially valuable for grazing by livestock were chosen for this study.

Paspalum centrale Chase is an annual and caespitose species 30–85 cm



Figure 1: Distribution map of occurrences of *Paspalum centrale* Chase. Source: GBIF portal

high (Clayton et al. 2012).

This is the least known of the species in this study.

Paspalum centrale is distributed only in Mesoamerica and Brazil, but

the report from Brazil is uncertain. It is rather a rare

species with few reports. The Mesoamerican Flora Project classified it as endemic to the region, and it has been reported from grasslands, savannas and lake beds at an altitudinal range of 0-1000 m a.s.l. (W3Tropicos, April 2012) (figure 1). Very little is known about its reproduction, environmental requirements, and factors that determine its distribution.

Paspalum virgatum L. is a perennial, caespitose and clumped densely species. Its Culms is robust; 100–200 cm high (Clayton 2012). *Paspalum virgatum* is a widely distributed species considered a weed (Plant database USDA 2012). It is native from Mexico to South America and is common in wet open areas, ditches and pastures in an altitudinal range of 0-1200 m a.s.l. (W3Tropicos 2012). It

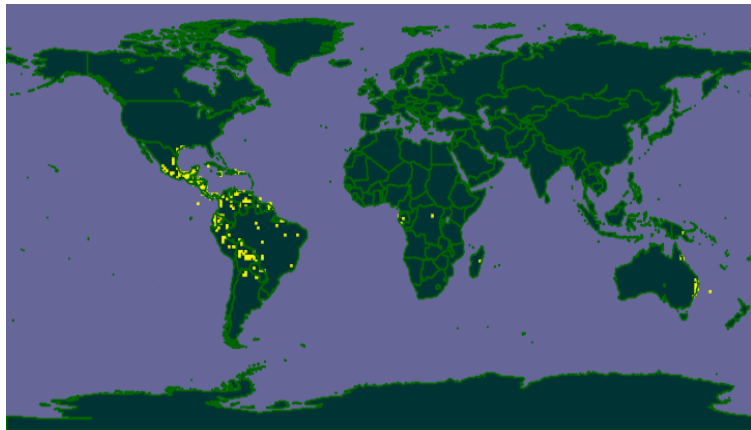


Figure 2: Distribution map of *P. virgatum*. Source: GBIF portal.

has been introduced in the southeastern

United States, where it grows primarily in disturbed areas and cultivated fields (Allen & Hall 2003). It has also been introduced in China and Australia (Heike 2012) (Figure 2). The seeds are destroyed by fire when they lie superficially, but some of them survive buried at 1 cm in the soil (Kellman 1980). *P. virgatum* is an allotetraploid species (Hojsgaard et al. 2009) that reproduces both by seeds and vegetatively by rooted stem segments (Sistach & Leon 1987b). It is consumed by the cattle only at the earlier stages of its life cycle. Later the weed becomes inedible due to its leaves with sharp margins and low nitrogen and high fiber contents (Sistach & Leon 1987b). *P. virgatum* is also useful in erosion control (Quattrocchi 2006).

Paspalum conjugatum P. J. Bergius is a perennial or annual strongly stoloniferous species 30-60 tall. It is a pantropical species, native to tropical America (Allen and Hall 2003). It is found in an altitudinal range of

0-2400 m a.s.l. (W3Tropicos 2012, Quattrocchi 2006). It can behave as an invasive and persistent weed. It grows in disturbed areas and at the edges of forests, along rivers, wet places and wet habitats (Quattrocchi 2006). *P. conjugatum* is a tetraploid species with both sexual and apomictic modes of reproduction (Hojsgaard et al. 2010). This species has different uses in Africa (JSTOR Plant Science 2012), and is sometimes used as lawn grass in tropical and subtropical climates (Allen & Hall 2003) (Figure 3). This species is used as forage for grazing or in cut-and carry systems, and is

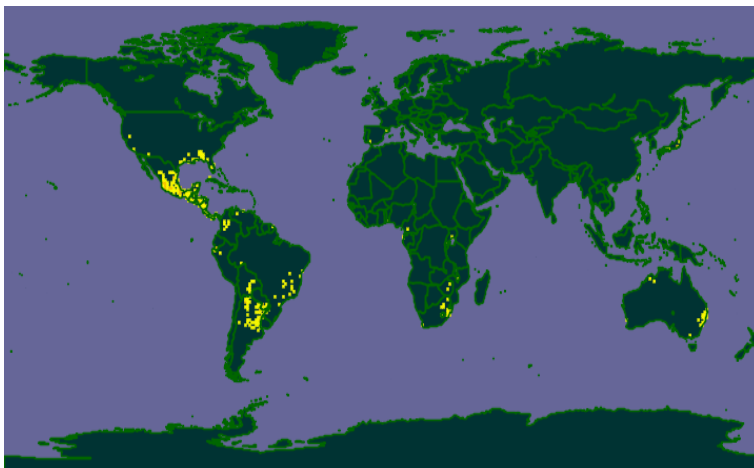


Figure 3: Distribution map of *P. conjugatum*. Source: GBIF portal.

rated as a very important natural forage plant in coconut plantation (Grassland species profiles FAO 2012). Because *P. conjugatum* is a shade

tolerant and can have an aggressive nature, the species makes a natural and uniform cover for plantations. After cultivation *P. conjugatum* can expand naturally, even beyond the natural biogeographic range (Acosta & Agüero 2002), and is a better forage plant if it never flower because its palatability is lower after the flowering stage (Beetle 1974). According to White et al. (1959) seeds tend to stuck in the throats of livestock and choke the animals. It has been reported that when the heavy growth produced during rainy seasons is eaten in large quantity, it disturbs the digestion of the cattle (McClelland 1915, cited by Beetle 1974). This species can grow in a wide variety of soil types but prefers wet and heavy soils (Heike 2012). With regard to pH, its performance is best

from 5 to 7 (Plant database USDA 2011). *Paspalum notatum* Fluggé is a perennial bunchgrass, polymorphic, vigorous, coarse, erect, often decumbent, low growing, creeping, forming dense turfs, rhizomatous, 40-70 cm high (Quattrocchi 2006, Clayton et al 2012). This species is native from Mexico through the Caribbean and Central America to Brazil and northern Argentina and is common in pastures and disturbed open areas. Its altitudinal range goes from 0 to 2350 m a.s.l. (Heike 2012). It has been

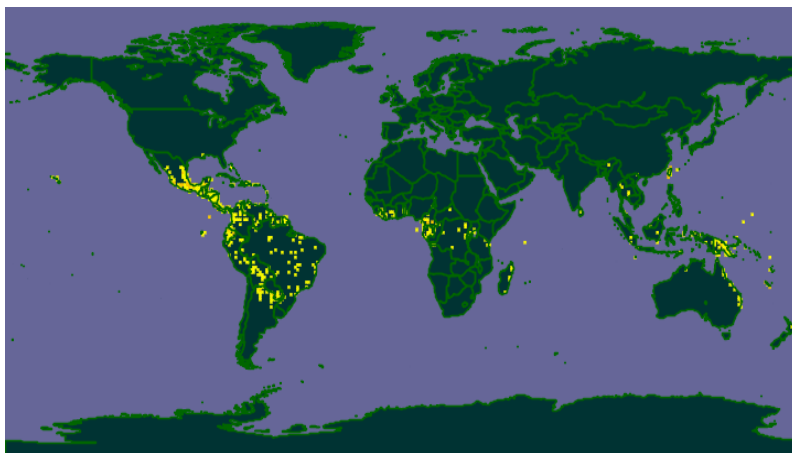


Figure 4: Distribution map of *P. notatum*. Source: GBIF portal.

introduced to the United States for forage, turf, and erosion control. It is now established, generally being found in disturbed areas and at the edges of forests in

the southeastern United States (Allen & Hall 2003, Houk 2009). It is also naturalized in Africa, Australia and elsewhere in tropics and subtropics (Cook et al. 2005) (Figure 4). *P. notatum* is a weedy species and highly invasive, but does not grow well in shade condition (Quattrocchi 2006). It is very drought tolerant due to its deep root system, and is fairly tolerant of flooding. It can tolerate light to moderate fire, but stands can be reduced by fire if there is an abundance of dry fuel (Cook et. al 2005). It is common on sandy or light textured soils in both its native and naturalized range, and sometimes extends onto clays. While preferring fertile soils, it can maintain dense stands on infertile soils (Houk 2009), probably due to nitrogen fixation in the rhizosphere. It grows on soils with pH of (4.3-) 5.5-

6.5 (-8.4) (Cook et. al 2005). It is a tetraploid species with both sexual and apomictic modes of reproduction. At least the 4x chromosome races of *P. notatum* have its sexual diploid conspecific counterparts (Hojsgaard et al. 2009).

With proper management *P. notatum* is a fair to good pasture and hay producing species, and can be used in woodland pasture systems (silvopasture). Forage quality depends on soil fertility and stage of growth. *Paspalum notatum* presumably has moderate tolerance to aluminium. Iron chlorosis can develop on less acid soils in spring and autumn. Some types, at least, are salt tolerant, withstanding up to 4,500 ppm NaCl in irrigation water. Photosynthesis and transpiration are reduced when NaCl levels reach 9,000-27,000 ppm. This species responds well to nitrogen fertilizer (Heike 2012).

Study sites

The natural vegetation of the regions where the study took place corresponds to studied are Tropical dry forest (Bullock et al. 1995), with semi-deciduous vegetation. Twenty eight tropical and subtropical forested ecoregions are represented in Central America (Lugo et al. 1981), and approximately half of the vegetation of Central America and the Caribbean is within the dry forest ecoregion (Holdridge 1967, cited by Lugo et al. 1981). Dry forests occur most commonly on coastal areas of low relief, and on the Pacific side of the central American land mass at elevations below 2000 m (Bullock et al. 1995). Currently, the majority of this

vegetation has been transformed into a silvopastoral landscape with a vegetation cover composed by assemblages of native and naturalized species including grasses, herbs and woody plants. The herbaceous cover are semi-natural grasslands, a term used herein to refer to a pastureland area covered by spontaneous vegetation that grows naturally after forest clearing or on fallow land and which is maintained by grazing management, including fencing and weed control. Semi-natural grasslands often occur in association with scattered trees, which are the major components of silvopastoral systems, the most outspread land-use form in the region. The grasslands consist mostly of various grass species of the genus *Paspalum* (Ospina 2010).

The study was conducted in three larger regions: 1.-The region in the municipality of Muy Muy, Río Grande de Matagalpa, Nicaragua ($12^{\circ}31'' - 13^{\circ}20''\text{N}$; $84^{\circ}45'' - 86^{\circ}15''\text{W}$) within an altitudinal range of 293 to 800 meters (Ospina 2010), henceforth called **Muy Muy**. 2. – The area in the Municipality of Belén, Rivas, Nicaragua ($11^{\circ}30'\text{N}$ and $85^{\circ}53'\text{W}$) (INIFOM 2005) within an altitudinal range of 51 to 170 meters above sea level, henceforth called **Rivas**. 3. - The wildlife refuge Río Escalante -Chacocente, Pacific –South region of Nicaragua ($11^{\circ} 30'33.0'' - 11^{\circ} 35' 28.5 \text{ N}''$; $86^{\circ} 08' 33.7 '' - 86^{\circ} 14' 43.1 \text{ W}''$) (MARENA 2008) at sites between 83 and 109 m a.s.l., henceforth called **Chacocente**

There is presence of livestock farming throughout the study regions but with some differences in the intensity and livestock management (Ospina 2010, Saucedo 2010, MARENA 2008). In Muy Muy livestock production is generally extensive, with an average-stocking rate of 1 animal/ha and pasture management consists of rotational grazing, fence maintenance

and weeding, either manually by chopping down weeds or recently by the use of herbicides (Ospina 2010). During the dry season, grazing frequency is irregular. In Rivas the main economic activities are farming, (main crops being rice, plantain, sugar cane, beans and sorghum) and livestock raising (INIFOM 2005 and Saucedo 2010). The third region is a wildlife refuge, but some presence of cattle occurs (MARENA 2008).

In Muy Muy the topography is undulating, with slopes between 5-40%. The dominant soil type is a grayish to black colored vertisol with high organic matter content in the upper horizons (5-8%), clayey subsoil, with a

pH between 5.9 and 6.8 in the topsoil, and relatively poor in phosphorous (2-10 ppm). In most cases, the soil has limited drainage during the rainy season (Ospina 2010). In

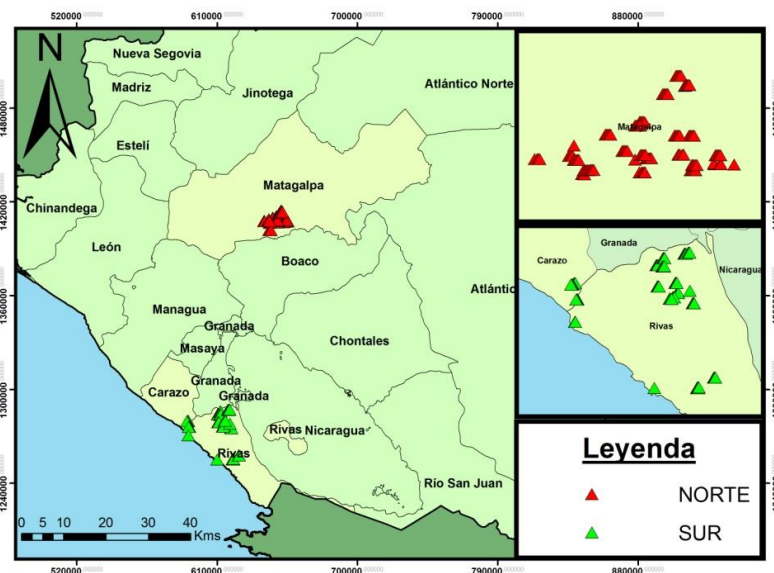


Figure 5. Location of sampling sites throughout the study area.

Rivas, the main topographic conditions are flat areas (19%) open slopes (41%) and mountain ranges (12%) (Saucedo 2010). The relief of the wildlife refuge Río Escalante-Chacocente is irregular, being a low-rise landscape; formed by a strip of beach of 11.6 kilometers that rises progressively toward the inner lands through a series of continuous small hills of 200 to 300 meters altitude (MARENA 2008).

The study regions are dominated by pasture with some remnants of secondary and riparian forest. In the mountain ranges some patches of primary forest are surrounded by coffee crops in Muy Muy and Plantain crops in Rivas. In previous studies, ten types of land use were characterized in Rivas (SILPAS 2009). Excluding some categories and adding the categories Primary forest and Coffee crop, the classification of habitat used in the study is shown in the table 1.

Table 1: *Types of land use/cover in the study area (adapted from SILPAS 2009).*

Land use	Description
Primary forest	Forest well conserved
Secondary forest	Closed tree cover. Riparian forests (forest vegetation along rivers/streams). Trees taller than 15 m and presence of an understory shrub layer. Riparian forest should be a minimum of 10 m on each side of the stream.
Coffee crops	Closed tree cover. Coffee is a shade growing shrub. The ground is constantly cleaned from herbs and other weeds
Tacotales	Vegetation covers predominantly of shrubs with presence of trees up to 12 m high.
Charrales	Vegetation cover dominated by shrubs of approx. 5 m high
Paddocks with trees	Dominant vegetation cover is grassland with scattered trees (tree cover > 5 %)
Paddocks without trees	Dominant vegetation cover is grassland with scattered trees (tree cover less than 5 %).

Field sampling

Three regions were sampled through a set of transects that covered the major environmental and land-use heterogeneity of the areas. Forty two, 500 m long transects, were laid out across the silvopastoral landscapes, covering a range of soil types, topography, land uses/land cover and vegetation structure. Along each of these transects, 5 plots, 20 x 20 m², with a separation of 100 meter were located and geo-referenced, the total number of plots was 205. The plots were located in an East-West and South-North direction.

Whenever a *Paspalum* target species was found, the accompanying species were recorded within the 20 x 20 m² plot. The non-target species were also listed in 11 plots where no occurrence of the target species was observed. The composition of the accompanying species at the plot was used as a proxy that summarized the local bio-physical environment, including management history. In each of those plots the environmental variables listed in table 2 were recorded. In addition, the abundance (basal cover) of the 4 *Paspalum* target species was assessed along a 20 meter long line divided in sections of 1 m. The meters number one, three, five, seven and nine were sampled. These lines were placed in the middle of the 20x20 m plot along the South-North direction. Here variables 6 and 8 listed in table 2 were measured. Whenever the line intersected any *Paspalum* species its basal area cover was recorded. When plots were located under tree crowns, the species of the tree was identified. When other *Paspalum* species, different from the *Paspalum* target species, was

found in the proximity of the sampling plots, it was collected and identified.

The physiological status of the plants was assessed by recording chlorophyll Ila fluorescence, an indirect measure of photosynthesis performance (Maxwell & Johnson 2000), and an indicator of the degree of stress experienced by the plant. The total number of plants assessed was 443. Within the 20x20 m² plots, three individuals of each *Paspalum* target species were selected. On each individual, a fully-developed and healthy leaf was selected, and deployed with a small clip that maintained the small portion of the leaf in darkness during 20 minutes, prior to recording the parameters. Then the unit Handy PEA Chlorophyll fluorometer (Hansateck Ltd., UK) was used to measure Fm/Fv parameters. This is a parameter widely used to indicate the maximum quantum efficiency of photosystem II. It is considered a sensitive indication of plant photosynthetic performance with healthy samples typically achieving a maximum Fv/Fm value of approx 0.85. Values lower than this will be observed on samples exposed to some type of biotic or abiotic stress (Maxwell & Johnson 2000).

The soil was sampled at level of 20 x 20 m² in a total of 20 plots. Five subsamples were collected with an auger from the uppermost 10 cm along the 20 meters line used for the target species basal cover sampling. These subsamples were mixed in order to get a pooled sample of the whole plot. The samples were stored in paper bags, dried and sent to the soil, water and plant laboratory of the International School of Agriculture and Livestock in Rivas, Nicaragua for analysis. The soil parameters assessed are listed in the Table 2.

Tabla 2: Variables measured at the plot (20 x 20 m²) and line (20 m) level

Abiotic variables	Classes/Units	Sample unit
1. Position	Tops, mid slope, foot hills, flat	20 x 20 m ² plot
2. Soil type	pH H ₂ O, pH KCl, C, N, P, CIC, soiltext, sand, silt and clay.	20 x 20 m ² plot
3. Soil moisture	Scale from 1-5 (very dry to flooded)	20 x 20 m ² plot
Biotic variables		
4. Type of habitat	Pastures with trees, pastures without trees, primary forest, secondary forest, riparian forest, charral and tacotal	20 x 20 m ² plot
5. Vegetation structure	Forest cover, understory cover, herbal cover	20 x 20 m ² plot
6. Cover of each <i>Paspalum</i> species	Measures of basal cover	20 m line
7. Vitality of <i>Paspalum</i> species	Chlorophyll Fluorescence	Leaves of <i>Paspalum</i> species in plot
8. Accompanying species	List of other species with the target species	20 x 20 m ² plot and 20 line

The field work was performed from in the rainy season, from June 1st to August 15th 2011.

Data analysis

Multivariate statistics were conducted with CANOCO (Ter Braak & Smilauer 2002), and InfoStat 2011 (Di Rienzo, Casanoves et al. 2011). Correlations, normality tests and contingency tables were conducted with InfoStat 2011. Finally, species accumulation curves were constructed with the program Stimates 8.2.0. (Colwell 2008) and plotted with Sigmaplot 2000 version 6 for Windows.

The normality of the data was evaluated with Shapiro test ($P \leq 0.05$).

To identify the patterns of plot grassland composition, the data on species assemblages of accompanying species were analyzed with multivariate

statistics (Detrended Correspondence Analysis DCA) using the environmental variables as passive variables. The scores of the plots on the DCA axis were used as proxies of habitat descriptors of the target *Paspalum* species. In order to advance in the interpretation of the vegetation patterns obtained through the DCA, the correspondence of the DCA axes with the target species and physical variables recorded in the plot was explored.

The patterns of soil properties variability was obtained with Principal Component Analysis (PCA). Chi square test ($P \leq 0.05$) was conducted to detect associations between the target species basal cover and environmental categorical variables (Position and Type of habitat). I took the first two principal components scores of this analysis and conducted a Spearman correlation analysis with the basal cover of the *Paspalum* target species.

Spearman correlation (interval -1:1), were used to evidence correlations among the target species basal cover and environmental continuous variables (Altitude, soil moisture, vegetation structure and soil type).

To assess the factors affecting the different species performance (total of *Paspalum* basal cover and average of vitality by species by plot), Spearman correlation was used.

The specimens were identified mostly with the keys of Flora de Nicaragua and Flora of Mesoamerica (W3Tropicos, Missouri Botanical Garden), identified by the author and the nomenclature follows the Flora of Nicaragua.

Results

Of the total of 205 plots, 17 were located in Chacocente, 118 in Muy Muy and 70 in Rivas. In sixty four of these, at least one of the four *Paspalum* target species occurred along the 20 m sampling line. In another three plots, at least one of the *Paspalum* target species occurred outside the 20 m line but inside of the 20x20 m² plot. Thus 67 plots had presence of at least one *Paspalum* target species. No *Paspalum* species was present in 127 plots, 17 in Chacocente, 46 in Rivas and 64 in Muy Muy. Eleven of the plots without presence of *Paspalum* species were sampled to record the accompanying species (table 4).

Table 4. Total of sampled plot with presence of *Paspalum* target species across the study sites. **Paspalum in 20x20 plot**, *Paspalum* species present inside the 20x20 plot. **Paspalum on line**, *Paspalum* species present on the 20 meters line. **No Paspalum**, plots without presence of *Paspalum* target species. **Species list only**, 20x20 m² plots with no occurrences of *Paspalum* target species where a list of other species was recorded. **CH**; Chacocente, **MY**; Muy Muy, **RV**; Rivas.

Sites	<i>Paspalum</i> in 20x20 plot	<i>Paspalum</i> on 20m line	Species list only	No <i>Paspalum</i>	Total
CH	0	0	0	17	17
MY	2	59	11	46	118
RV	1	5	0	64	70
Total	3	64	11	127	205

Regional Distribution and diversity of plants

The total number of species recorded in this study was 185 belonging to 54 families (Appendix I). Eight of these were *Paspalum* species. The most species rich families were *Poaceae* and *Fabaceae* with 28 and 27 species respectively. Some other families were represented by 7 to 14 species (*Cyperaceae*, *Rubiaceae* and *Malvaceae*) (Figure 6a). Thirty-four species

were trees, 25 were shrubs and 126 herbs including *Paspalum* and other grasses species. Seventy nine species were recorded only in the 20x20 m² plots and not in the 20 meters line. These species were mainly trees and shrubs. The remnant 105 species were present in the 20x20 m² plots and 20 m line. The total number of species recorded in Rivas was 49, ten of them only there. The total number of species found only in Muy Muy was 174. The total of shared species among these two localities was 31. Nineteen exotic species were present in the study area, seven of them in Rivas and all of them in Muy Muy. The origin of another three species is not clear (Appendix I). The species accumulation curves showed that increasing the sampling is possible to increase the richness of species, especially in Rivas. The sampling effort was greater in Muy Muy (118 plots) than in Rivas (70 plots) (Figure 6b). The average of species by plot was 22 in Muy Muy and 14 in Rivas.

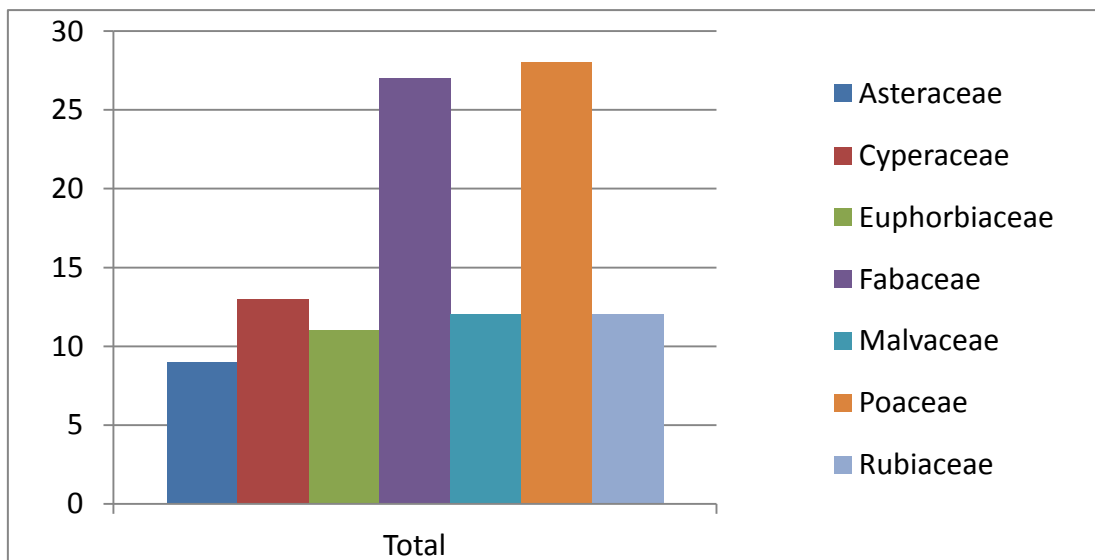


Figure 6. Species richness by family.

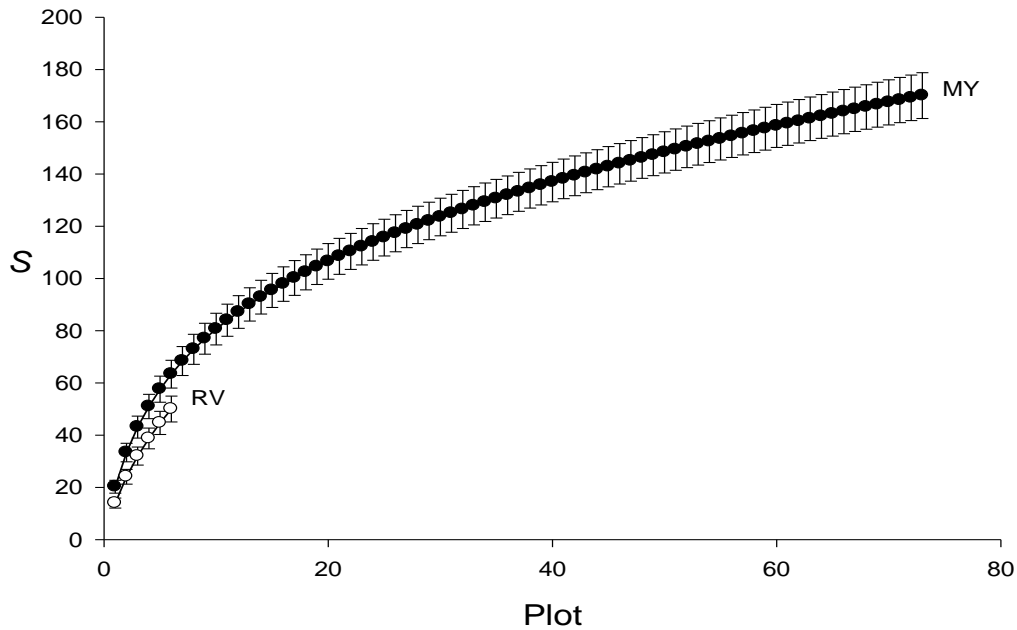


Figure 7. Accumulation species curvas. Number species (S) and number of sampled plots. MY; Muy Muy, R; Rivas.

In this study eight species of *Paspalum* were found, five of them on the 20 meters line and in the 20x20 m² plots. One of the species found in the plots, *Paspalum costaricense* Mez, was found just once. The two other species only found nearby the sampling plots were *Paspalum convexum* Humb. & Bonpl. ex Flügge and *Paspalum paniculatum* L. Of the remaining species *Paspalum dilatatum* Poir, was found in a paddock not sampled (Table 5). *Paspalum plicatulum* Michx., reported by Ospina (2005) in Muy Muy, was not found. Rivas and Muy Muy shared three species and each one had a total of five species. Just one species of *Paspalum* was present in Chacocente, *Paspalum dilatatum* Poir. It was only found in Chacocente and it is the first record of this species for Nicaragua (Appendix II).

Table 1. *Paspalum* species and sampling sites. Rivas and Muy Muy, each one has five species, three of them shared. Two species were distributed exclusively in each site. The total of species is eight.

Species	Site
<i>Paspalum centrale</i> Chase	Muy Muy
<i>Paspalum conjugatum</i> P. J. Bergius	Muy Muy
<i>Paspalum convexum</i> Humb. & Bonpl. ex Flüggé	Muy Muy/Rivas
<i>Paspalum costaricense</i> Mez	Rivas
<i>Paspalum notatum</i> A. H. Liogier ex Flüggé	Muy Muy/Rivas
<i>Paspalum paniculatum</i> L.	Rivas
<i>Paspalum virgatum</i> L.	Muy Muy/Rivas
<i>Paspalum</i> CF dilatatum	Chacocente

The eight *Paspalum* species found in this study occupy an altitudinal range from 20 to 800 m a.s.l. *Paspalum dilatatum*, occurred at 20 m a.s.l. The four *Paspalum* target species were most abundant between 300-576 m a.s.l. At this range all of them were present. Below this altitudinal range only *P. notatum* was present and above this range only *P. conjugatum* occurred.

According to the Shapiro test, just the basal cover of *P. virgatum* with $p=0,37$ was normally distributed. The basal cover and fluorescence data from the other *Paspalum* target species, were not normally distributed (Table 6).

Table 6. Normality of the *Paspalum* basal cover and fluorescence data. The Shapiro wilks test ($p \leq 0.05$) shown that, excepting basal cover of *P. virgatum*, the data did not follow a normal distribution.

Variable	N	Media	D.E.	W*	p(Unilateral D)
Paspencov	16	27,06	38,35	0,68	<0,0001
Paspconcov	16	31,59	33,18	0,78	0,0005
Paspnotcov	45	58,66	59,36	0,83	<0,0001
Paspvircov	9	24	15,8	0,9	0,3719
Paspconflou	19	5,01	18,52	0,29	<0,0001
Paspnotflou	51	0,72	0,1	0,74	<0,0001
Paspvirgflou	20	0,76	0,06	0,66	<0,0001
Paspcenflou	23	0,75	0,05	0,85	0,0034

Local factors determining *Paspalum* target species distribution

Habitat type and topography There were no sampling site with all four *Paspalum* target species coexisting, either at the 20 m line level or at 20x20 m². At 20 m line level three species occurred just four times, twice in the combination *P. notatum*-*P. centrale*-*P. virgatum*; once in the combination *P. conjugatum*-*P. notatum*-*P. virgatum*; and once in the combination *P. conjugatum*- *P. centrale*-*P. virgatum*. Also in the 20x20 m² plot, just three species of *Paspalum* occurred together and the combination most frequent was *P. notatum*-*P. centrale*-*P. virgatum*, (9 times).

No *Paspalum* target species was present in primary forests, secondary forests and tacotales. All the *Paspalum* target species were present in paddocks used for cattle grazing. *Paspalum centrale* and *P. notatum* was present in charrals (three times and twice respect.) and *P. notatum* in riparian forests (twice). *P. conjugatum* was present in riparian forests, coffee plantations and at the edge of primary forest, but it was not

recorded in any of the sampling plots, only by casually observations. In the category Other habitats (Table 7), are habitats without presence of *Paspalum species* and with less than three plots sampled. The habitat with highest frequency of *Paspalum* (38) and most sampled plots was paddocks with trees (73) followed by open paddocks (59 and 25). The total number of habitats with presence of at least one *Paspalum* target species was 67 (Table 7).

Table 7. *Sampled plots sites and habitats. The habitats with black letters are sites without presence of any Paspalum species. Habitats with white letters are the habitat with presence of at least one Paspalum species. Total number of sampled plots, and number of plots with presence of Paspalum target species (in brackets). CH; Chacocente, MY; Muy Muy, RV; Rivas. Under the category other, are the habitats without presences of Paspalum species and less of three plots sampled.*

Site	Coffe crop	Primary forest	Riparian forest	Secondary forest	Charral	Paddocks with trees	Open Paddocks	Tacotal	Other	Total
CH		3	2	2	5	1	3		1	17
MY	4	3	6	1	12(1)	52(37)	29(21)	3	8	118(61)
RV		4	8(1)	4	3	20(1)	27(4)		4	70(6)
Total	4	10	16(1)	7	20(1)	73(38)	59(25)	3	10	205(67)

All the topographic position classes had at least one of the *Paspalum* target species in one of the sites (Table 8). In Muy Muy at least one of the *Paspalum* target species was present across all the classes. In Rivas only middle slopes and flats had *Paspalum* spp. Highest records of *Paspalum* target species were in middle slopes (27) which also was the class with most plots sampled (80). The highest frequency of *Paspalum* target species was in Muy Muy (61). Except the class flat topography, which had more plots sampled in Rivas than the other regions, the highest numbers of plots sampled across the classes were in Muy Muy. *Paspalum conjugatum* was not present in top slope and *P. virgatum* was not present

in bottom slope. The species *P. notatum* and *P. centrale* were present in all the classes of this category. *Paspalum notatum* was the most frequent species across the classes.

Table 8. Sampling sites and topographic position. The numbers in brackets represent the total number of sample plots with presence of at least one Paspalum target species by each class in the sites. **CH**; Chacocente, **MY**; Muy Muy, **RV**; Rivas. Under the category **other**, are the habitats without presences of Paspalum species and less of three plots sampled.

Sites	Top slope	Middle slope	Bottom slope	Flat	Other	Total
CH	2	10		4	1	17
MY	15(9)	55(26)	25(13)	20(12)	3	118(61)
RV	6	15(1)	8	40(5)	1	70(6)
Total	23(9)	80(27)	33(13)	64(17)	5	205(67)

The Chi square test ($P \leq 0.05$), between frequency of occurrences of *Paspalum* target species, and habitat type and topographic position, suggested a correspondence between the species *P. centrale* and the conditions Charral and Mid slope, and among *P. conjugatum* and the condition Mid slopes (Table 9). The other species did not show any correspondence with the variables.

Table 9. Significant Chi square from contingency tables between frequencies of the Paspalum target species and habitat type and topographic position ($P \leq 0.05$).

Species	Slopes	Charral
Pascent	0,0078	0,005
Pasconj	0,03	

Vegetation assemblies and soil

A Detrended Correspondence was performed. This analysis was done with and without the presence of trees in the plots, excluding the sampling

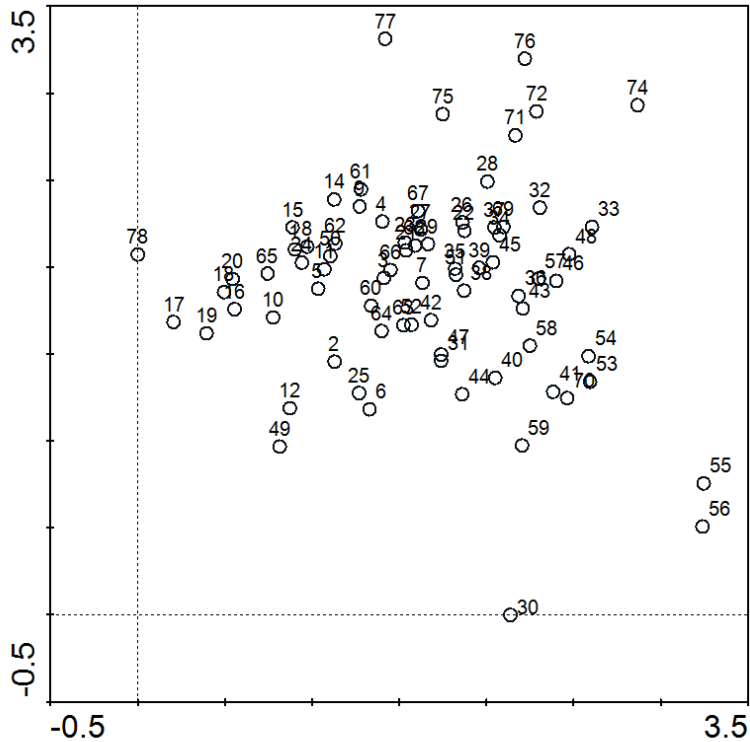


Figure 7. DCA between sampling sites and accompanying species including trees with environmental continuous variables as passives. The circles represent sampling sites.

sites MY303 and RV103.

In the case of the analysis including the presence of trees (Figure 7), the combination of the first two axes explained 8.4 % of the variation. When the analysis was conducted without including trees, the two first ordination

axes together explained 9.8 % of the variation.

This means that the

floristic composition of the plots are homogeneous, despite that, is possible to appreciate the species following a gradient along the axis 2, differences drove by forest cover and altitude. The altitude showed two significant Spearman correlations (p less than 001), one negative with basal cover of *P. notatum* (-0,42) and the other positive with the basal cover of the *P. conjugatum* (0,56). The axes 1 had not showed clear factors of variation. There is no clear clustering of plots, indicating that the variation in plot species composition (defined by the presence or absence of species) is gradual, with no major differences in the pool of species

present in the different areas. However, some regional differentiation is evident. Plots from Rivas (circles 73-77) were grouped at the top of the ordination diagram. Two plots from Muy Muy (circles 71 and 72) were similar to the Rivas sites. *P. notatum* is the only one target species present in these sampling sites. These sites were located at the lowest altitude of the study regions associated to the species *Cyperus iria* L., common in Rivas but scarce in Muy Muy. A distribution pattern of the target species is evident in the DCA (Fig 7). *Paspalum notatum* was diminishing from the top of the diagram where the Rivas and low altitude Muy Muy sampling sites are placed, going down through an intermediate zone of coexistence of the four target species, to the circle 30 where just *P. conjugatum* was occurring associated with the species *Desmodium sp*, *Eleusine indica*, *Crussea sp* and Graminea desconocida. In this intermediate zone *P. conjugatum* appear together with *P. notatum* (circles 41), then, is augmenting its frequency through the plots 58, 44 and 59. The plots 53-56 are close to each other and they are plots where no *Paspalum* target species were recorded.

The correlation analysis of the DCAs axes of variation test showed a positive correlations with *Paspalum conjugatum* (Ax1trees; $r=0,39$, $p=5,7$ E-04 and Ax1notrees $r=0,39$, $p=4,7$ E-04); negative correlations with *P. centrale* (Ax1tree; $r=-0,55$, $p=2,8$ E-07 and Ax1notree $r=-0,54$, $p= 4,40$ E-07) and negative correlations with *P. notatum* (Ax1tree; $r=-0,48$, $p= 1,10$ E-05; Ax2tree $r=0,36$, $p=1.3$ E-03; Ax1notree $r=0,39$, $r=1,10$ E-05; Ax2notree $r=0.37$, $p=1$ E-03). *Paspalum virgatum* did not show any significant correlation (Table 10). In the table 10, the numbers under the principal

diagonal are the Spearman coefficient values (r) and the numbers above the diagonal the probabilities associated to the test (p).

Table 10. Spearman correlation Paspalum target species and scores from the first two DCA axes of variation. The numbers under the principal diagonal are the r values and the values above the diagonal are p values. Stars indicate significant values

	Paspcen	Paspcon	Paspnot	Paspvir	AX1tree	AX2notree	AX1notree	AX2notree
Paspcen	1	0,11	1,70E-03	0,49	2,80E-07*	0,52	4,40E-07*	0,14
Paspcon	-0,18	1	6,50E-06	0,92	5,70E-04*	0,35	4,70E-04*	0,05*
Paspnot	0,35	-0,49	1	0,86	1,10E-05*	1,30E-03*	1,10E-05*	1,00E-03*
Paspvir	0,08	0,01	0,02	1	0,62	0,53	0,49	0,14
AX1tree	-0,55	0,39	-0,48	-0,06	1	0,89	0	0,5
AX2tree	0,07	-0,11	0,36	0,07	0,02	1	0,61	2,80E-11
AX1notree	-0,54	0,39	-0,48	-0,08	0,97	0,06	1	0,49
AX2notree	0,17	-0,23	0,37	0,17	-0,08	0,77	-0,08	1

Soil

A principal component analysis was conducted. The first two principal components express together 64.1 % of the variation and its eigenvalues were 3.66 and 2.11 respectively. The biplot shows that the variables CEC (Cation Exchange Capacity) and Clay, were the main components affecting axis one (PCA-1). High values of these variables were associated with high PCA -1 scores. High values of silt, Sand, N (nitrogen) and C (carbon), were associated with low scores on PCA-1. The second axis derived from the Principal Component Analysis (PCA-2) was driven by plot differences in soil pH. High values of pH_{H₂O} (pH in water), pH_{KCl} (pH in Potassium Chloride) and P (Phosphorous) were associated with high PCA-2 scores. There was a clear regional differentiation of the plots. All Rivas plots (RV), were positively correlated with the variables Clay and CEC on the PC-1. In general Muy Muy plots had low scores on PCA-1 except for MY103,

MY204, MY 2201 and MY 2303, whose soils were similar to those in the Rivas plots. The sites MY 1203 were correlated with the variables Sand; and the sites MY 903 and MY 802 with the variable Silt. A group of sampling sites was negatively correlated with the variables C and N (MY1601, MY1703 and 1804); whereas other sites (MY 1305 and 1101) were positively correlated with P (Figure 7). The first two principal components scores was used in a Spearman correlation with the basal cover of the *Paspalum* target species.

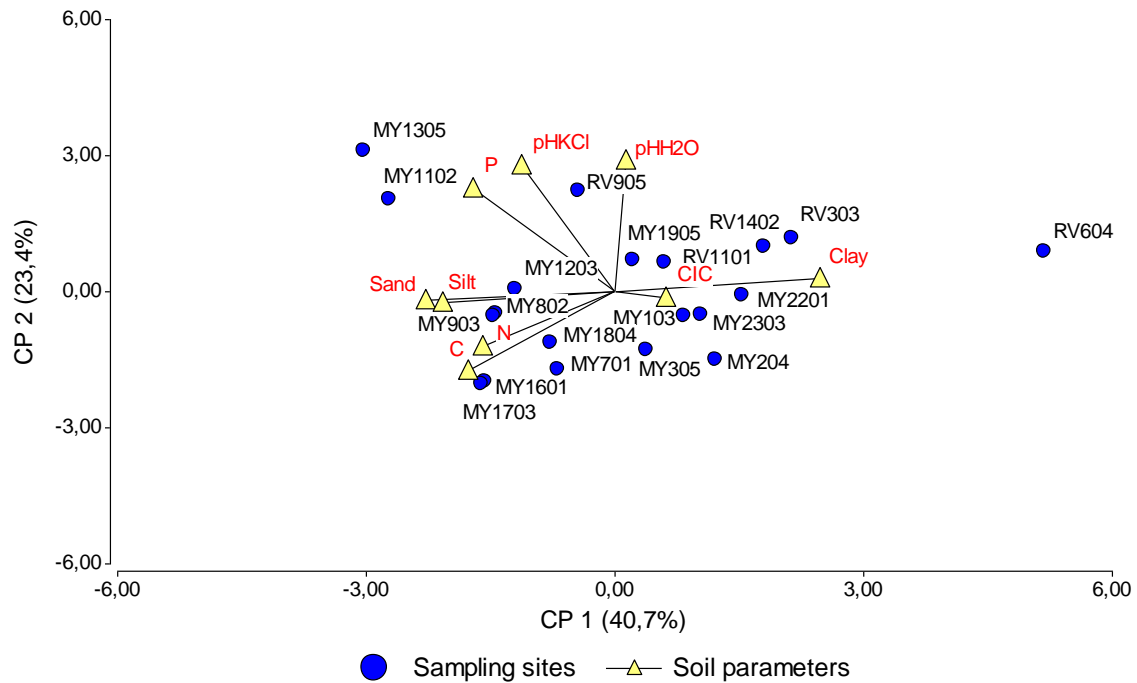


Figure 6. Biplot PCA Soil parameters and sampling sites: MY, sampling sites from Mui Mui; RV, sampling sites from Rivas. Soil Parameter: C and N, percentage of Carbon and Nitrogen in weight; P, parts per million or Phosphorus; pHKCl and pHH2O, pH in Potassium chloride and pH in water; CEC, cation exchange capacity; Sand, Silt and Clay, percentage of particles of sand, silt and clay in the first 10 cms of the soil.

In the PCA diagram (Fig 7) is possible to see a gradient, with *P. notatum* and *P. conjugatum* in the opposite extremes. Starting on the axes 1 from the left in the side of MY2201 and MY2303 sampling sites, where just

Paspalum notatum was present and clayish soil predominate; going to sites MY204, MY305 and 701 where *P. notatum* and *P. centrale* coexisted in a zone with low pHKCl. Then, passing to the site MY1601 where *P. notatum* and *P. conjugatum* co occurred. Following toward the right, there were a zone (MY1804, MY903 and MY802) where *P. virgatum* was common and coexisted with *P. notatum* and *P. centrale*. Finally ascending on the axes two where just *P. notatum* is present (MY1203, MY1102 and MY1305). Here were sandy and loam soils and influence of P and pHKCl. *Paspalum conjugatum* had positive correlation with pHKCl and pHH2O and it occurred in some plots with higher values of those

The spearman correlation between basal cover of the *Paspalum* target species and the first two PCA axes shows a strong negative correlation among *P. conjugatum* and PC-1, and strong positive correlation between *Paspalum notatum* and PC-1 (Table 11).

Table 11. Spearman correlation PCA soil scores and basal cover of *Paspalum* target species. PC1 and PC2, scores from the first and second principal components of the PCA. The numbers under the principal diagonal are the *r* values and the values above the diagonal are *p* values. The stars indicate significant values.

	Paspcen	Paspcon	Paspnot	Paspvir	PCA1soil	PCA2soil
Paspcen	1	0,1	1,7E-03	0,53	0,58	0,09
Paspcon	-0,18	1	6,50E-06	0,96	0,02*	0,15
Paspnot	0,35	-0,5	1	0,92	0,01*	0,33
Paspvir	0,07	0,01	0,01	1	0,87	0,51
PC1soil	0,15	-0,58*	0,63*	-0,05	1	0,96
PC2soil	-0,44	0,38	-0,26	0,18	-0,01	1

In correlations between individual soil parameters (Appendix III) and basal cover area of *Paspalum* target species (Table 12). *Paspalum centrale* was negatively correlated with pHH2O, pHKCl and content of P (Phosphorous). *Paspalum conjugatum* had a negative correlation with silt content, and

strong positive correlations with pH in water (pHH₂O), pH in KCl (pHKCl), and content of clay. *Paspalum notatum* had strong negative correlation with pHKCl and silt content, and positive correlation with clay content. Finally, *P. virgatum* had no correlation with any of the soil parameters. The parameters: C (Carbon content), N (Nitrogen content), CEC (Cation Exchange capacity), and Sand content, were not included in the table 12, because they had not a significant correlation with the Paspalum species basal cover.

Table 12. Spearman correlation basal cover of Paspalum target species and individual soil parameters. The numbers under the principal diagonal are the *r* values and the values above the diagonal are *p* values. The stars indicate significant values.

	Paspccn	Paspcon	Paspnot	Paspvir	pHH ₂ O	pHKCl	P	Silt	Clay
Paspccn	1	0,11	1,70E-03	0,49	0,05*	0,04*	0,04*	0,48	0,62
Paspcon	-0,18	1	6,50E-06	0,92	0,02*	0,04*	0,22	0,02*	0,04*
Paspnot	0,35	-0,49	1	0,86	0,12	0,03*	0,17	0,03*	0,03*
Paspvir	0,08	0,01	0,02	1	0,97	0,72	0,58	0,72	0,89
pHH ₂ O	-0,5	0,57*	-0,4*	0,01	1	1,60E-03	0,02	0,49	0,73
pHKCl	-0,52*	0,51*	-0,53*	0,1	0,72	1	3,90E-04	0,42	0,54
P	-0,52*	0,32	-0,36	-0,15	0,57	0,78	1	0,41	0,38
Silt	-0,19	0,58*	-0,55*	0,1	0,19	0,22	0,22	1	6,50E-05
Clay	0,14	-0,52*	0,54*	-0,04	-0,09	-0,17	-0,23	-0,83	1

Species status based on basal cover and physiological performance

The total of basal covers by species and its average per meter is presented in the Table 13. The highest basal covers were recorded for *P. notatum* (2639,64 cm) and *P. conjugatum* (505,5 cm) . The highest average basal

cover was observed in *P. notatum* (8,30 cm/m). During the field work it was observed that this species is able to form extended and continuous carpets, whereas *P. conjugatum* tends to occur spread out on small spots. *Paspalum centrale* and *P. virgatum* had a very scattered occurrence in the plots. They never form a continuous cover and their average cover per meter were low (1.36 cm/m and 0,69 cm/m, resp.)

Table 23. Total and average cover of *Paspalum* species basal cover in cm meter⁻¹

Species	Total	Average per meter
<i>Paspalum centrale</i>	432,9	1,36
<i>Paspalum conjugatum</i>	505,5	1,58
<i>Paspalum notatum</i>	2639,64	8,30
<i>Paspalum virgatum</i>	216	0,67
Total	3794,04	11,94

The Spearman correlation of basal cover between species showed a negative correlation among *P. notatum* and *P. conjugatum* (-0.49), but with a significant p value (<0.001). And a positive correlation between *P. centrale* y *P. notatum* (0,35) with a significant p value also (<0.001) (Table 14).

Table 14. Spearman correlation basal cover of *Paspalum* species among themselves. The numbers under the principal diagonal are the *r* values and the values above the diagonal are *p* values. The stars indicate significant values.

	Pascencov	Pasconcov	Paspnotcov	Paspvircov
Pascencov	1	0,11	1,70E-03*	0,49
Pasconcov	-0,18	1	6,50E-06*	0,92
Paspnotcov	0,35*	-0,49*	1	0,86
Paspvircov	0,08	0,01	0,02	1

The Spearman correlation between Fluorescence and basal cover of *Paspalum* target species showed strongly significant correlations between all the species (Table 17). The averages of fm/fv values for each species

were: *P. notatum* (0,72), *P. centrale* (0,75), *P. conjugatum* (0,76) and *P. virgatum* (0,77).

Table 35. Spearman correlation Fluorescence and Paspalum basal cover. Numbers out of brackets are the *r* values and numbers in brackets the *p* value.

	Pascencov	Pasconcov	Pasnotcov	Paspvircov
Pascenflou	0,8 (0)			
Pasconflou		0,98 (0)		
Pasnotflou			0,81 (<0.001)	
Paspvirgflou				0,92 (<0.001)

Discussion

Regional distribution and diversity of plants

This study assessed the distribution of the four *Paspalum* species at different scales. At the regional scale, species segregation in grasslands has been interpreted as governed by environmental heterogeneity and significantly associated with land use (Reitalu 2008). The regions of Chacocente, Muy Muy and Rivas were clearly different. These differences, at least in part appear to rely to the land uses of each region. The environmental requirements of the four *Paspalum* species (W3Tropicos 2012, Heike 2012, Allan & Hall 2003, and Quattrocchi 2006) would allow them to occur throughout the study regions. However, all four target species were present only in Muy Muy; two of them in Rivas and no one in Chacocente.

The differences in distribution could also be a result of uneven sampling among regions. Sampling in Chacocente, was incomplete because there were two very distinct kinds of land cover/land management, protected area and livestock areas with cultivated pastures. The semi natural grasslands occurred inside of the protected area and it was not possible to sample. Therefore, the majority of the Chacocente sampling was in areas used for livestock raising on cultivated pastures which were dominated by *Hyparrhenia rufa* (Nees) Stapf. I visited only one seminatural grassland inside the Wildlife Refuge Río Escalante Chacocente, where I found *Paspalum dilatatum* Poir. This species is characteristic due to the presence of fringe and long hairs along the margins of the upper glume and lower

lemma. It is native from Argentina and Brazil and widely cultivated and naturalized in warmer climates of the world (W3Tropicos 2012). The occurrence of *Paspalum dilatatum* in Chacocente (Appendix III) is the first time the species has been reported to Nicaragua. It has, however, been reported from other countries in Central America (Zuloaga & Morrone 2003).

The regional differentiation in richness and distribution patterns between Rivas and Muy Muy of the species that co-occur with the target *Paspalum* species can be explained by management and land use history. With semi natural grasslands with native grasses species and less development of agricultural uses of the land in Muy Muy whereas in Rivas agriculture and livestock raising was more intense. Dijkstra et al. (2007) showed that species richness in semi natural grasslands is negatively affected by agricultural nutrient enrichment. Cousin (2009) reports that grazing ex-arable fields contain a fraction of the plant species richness confined to semi natural grasslands. And it will most likely take a long time for grazed ex-fields to reach the same species composition or the same high species diversity as traditionally managed semi-natural grasslands, due to residual nutrients and soil compaction. Cousin also reports that site location within a landscape and vicinity to species-rich grasslands had more species compared with those neighboring less species rich semi natural grasslands. Species-rich habitats in the surrounding landscape function as a source for spontaneous dispersal into abandoned ex-arable fields (Ruprecht 2006).

Plant growth and interactions can differ across landscapes as a consequence of heterogeneous soil type, management practices and

topography (Henry et al. 2009). One of the factors influencing the differences in distribution pattern of *Paspalum* target species between Rivas and Muy Muy appears to be the soil. The soil principal component analysis showed almost all the sites from Rivas grouped around the variable Clay. Some sampling sites from Muy Muy also corresponded to sites with high clay content in the soil. Sampling sites with clayish soils shared the presence of *P. notatum*. This species is a deep rooted perennial species adapted to a wide range of soils, but is reported to prefer sandy soils (Houck 2009) although sometimes it can grow on clay (Cook et al 2005). It was present in Rivas but with less frequency than in Muy Muy, where the soils in general had higher sand content, and where it is more productive (Houck 2009). In contrast *P. conjugatum* is known to perform better in clay soils (Heike 2012). In general the soil conditions in Rivas are suitable for the occurrence of *P. conjugatum* but it did not occur there.

Paspalum centrale was not present in Rivas and *P. virgatum* was rare. Despite to be considered common in disturbed and open habitats like paddocks, *P. virgatum* did not appear either at 20m line or at 20x20 plot level, just in the vicinity of the sampling plots. One reason for this pattern could be the management of the landscape in Rivas. It has been shown that management and land history in grasslands are more important to species richness than local soil properties (Cousin 2009, Reitalu 2008). Rivas is a very disturbed it is mainly an area for crop farming agriculture and livestock raising (INIFOM 2005) with a constant rotation between these activities. The use of exotic grasses is extended and grasslands are homogenous and dominated by the African grass species *Hyparrhenia rufa* (Nees) Stapf. In contrast, in Muy Muy the agriculture is very limited.

Paspalum centrale had been reported before from Rivas close to study the sites (W3Tropicos 2012), but in more heterogeneous and better conserved habitats. Thus, at regional scale the absence of *P. conjugatum*, *P. centrale* and the scarcity of *P. virgatum* in Rivas could be explained in terms of management and land use history. On the other hand the presence of *P. notatum* appears to be a generalist species with the capacity to thrive under condition of regular disturbance

The uneven sampling effort between Muy Muy and Rivas may also add to the differences because the sampling effort was greater in Muy Muy. However the sampling effort in Rivas was not small, the number of sampled plots was 70 in Rivas and 118 in Muy Muy. In fact the topographic condition flat was better sample in Rivas than in Muy Muy. The average or species by plot was also higher in Muy Muy. Then the richness of the accompanying species could increase but the conditions of the landscape seem not conducive to the occurrence of the remnants *Paspalum* target species. Even in Muy Muy in very disturbed places such tacotales or charrales or crops, the target species did not occur or occurred few.

Local factors determining Paspalum target species distribution

The occurrence of species at local level has been associated with environmental factors in other studies. The degree of species segregation was significantly associated with the plots positions within the grasslands patches (Reitalu 2008) and *P. notatum* had more biomass in top slope

position, related with highest phosphorus accumulation. These values have a significant decrease with decreasing slope (Sigua et al. 2011). Landscape position may be one of the dominant factors of soil properties under hill slope because it influence runoff, drainage, soil temperature, and consequently soil formation (Aandahl 1948). Concentration of the Total Inorganic Nitrogen (TIN) varied significantly with landscape position and soil depth. Top slope and surface soil had the greatest concentrations of TIN. The greatest forage availability of *P. notatum* and the highest N uptake were observed from the top slope position (Sigua et al. 2010). In the present study, *P. notatum* did not show any correlation or association with P or topographic and habitat condition, but it was frequent in flat conditions. Foot hill is also a flat topographic condition but located at the base of a steep slope. Adding the frequencies of this species in these two topographic positions, *P. notatum* is frequent in flat positions. Ospina (2005) founds association between *P. notatum* and flat conditions, in the Muy Muy region. Sigua et al (2010) addressed his results to the grazing behavior of the cattle which is more prone to graze at bottom slopes affecting the herbage mass production. In this study maybe the separation of the flats in two topographic conditions, could influence the no statistic association of this species with the class flat.

Due to the shoot and rhizome growth, *Paspalum notatum* has been reported not to be affected by any soil humidity level regardless of soil type or competition (Henry et al. 2009). This is also consistent with the general results of this study. This species was present in all categories of soil and soil humidity levels. However, in this study it showed a negative correlation with soil silt content and a positive correlation with clayish soil.

As *P. notatum* is reported to perform better in sandy soils (Houk 2009) more frequency of the species was expected in loam soil (with more sand content) but it was not like this. Loam soils are fertile soils and *P. notatum* performs better in soils with relative low fertility than other forage grasses (Houk 2009). This is consistent with the results of this study. Although *P. notatum* prefers sandy soils it can occur at clayish soil (Houk 2009). A limiting factor to the *P. notatum* distribution could be pH. *Paspalum notatum* had a negative correlation with pHKCl and occurred at sampling sites with acid soil (pHKCl= 4.66-4.85) but not in the sampling points with more neutral soils (pHKCl= 5.64-6.23). These values were within the pH range reported for *P. notatum* by Cook et al (2005), but *Paspalum notatum* did not occur there.

Paspalum conjugatum is a species known as wet tolerant and growing in a wide variety of soils (Quattrocchi 2006, Heike 2012, Maciel 2010). However in this study *P. conjugatum* had some preferences for soil parameters but not with soil moisture. *Paspalum conjugatum* was associated with mid slopes, topographic conditions reported to have low in soil humidity (Sigua et al. 2010). In this study mid slope was the position with lowest values of soil moisture (data not showed). Beetle (1974) states that *P. conjugatum* can sometimes tolerate drought. The positive correlation of *Paspalum conjugatum* with pHKCl and pH_{H2O} is also in accordance with the pH ranges reported before (Plant database USDA 2011). This species showed however, a negative correlation with clay which was unexpected. It could perhaps be due to the competition with *P. notatum* and *Axonopus compressus* (see below).

The knowledge about the ecology of *Paspalum centrale* is poor, but in this study it showed many correlations with the environmental factors, especially with soil type. This can be interpreted as a sign of good adaptation of this species to the local conditions. *Paspalum centrale* has been rarely recorded from paddocks and grasslands and it was rare also in this study. It was associated with mid slopes and Charral and had also a small but significant negative correlation with the soil moisture, which explains the correlation with the mid slope normally considered as a place low in soil humidity (Sigua et al. 2010). It is present throughout the topographic positions in Muy Muy but with low abundance. It is in accordance with the expectations of this study.

The absence of correlations of *Paspalum virgatum* with any environmental variable or with the other target species can be interpreted as a sign of generalist behavior. As this study expected, it was wide spread but with low abundances in the study regions. However, opposite the results of Ospina (2005), *P. virgatum* was not seen in riparian environments. This species is perennial, robust, caespitose and densely clumped and is consumed by the cattle only at the earlier stages of its life cycle. In later stages the plant becomes less palatable (Sistach & Leon 1987b). For this reason its presence is avoided by the producers, many times they remove it and then it is marginally present in Paddocks.

At plot level in Muy Muy just one combination of three *Paspalum* target species occurred more than once, *P. centrale*-*P. notatum*-*P. virgatum*. The distribution of *P. centrale* and *P. notatum* was positively correlated and they tend to occur together, which it did across all the topographic

conditions of this study. The distribution of these two species did not show any significant correlation with *P. virgatum*.

The distribution of *P. conjugatum* and *P. notatum* was negatively correlated. Beetle (1974) points out that these two species belongs to different stages in the ecological succession. However, they co-occurred in some plots. Except for *P. virgatum*, soil is a very important variable for the target species of this study and *P. conjugatum* had exactly the opposed correlations as *P. notatum* had for the same parameters. *Paspalum notatum* was positively correlated with the scores from the first principal component axis while *P. conjugatum* was negatively correlated with it. They are thus prone to occur in soils with very different characteristics, reinforcing the results of this study.

Altitude was strong and positively correlated with *P. conjugatum* and negatively with *P. notatum*. The first one occurred at high altitudes and generally in paddocks surrounded by forest or forested crops, and the second one preferentially at medium and low altitudes with sparse tree cover. The forest cover was not significantly correlated with any of the target species. Beetle (1974) and Acosta & Agüero (2002) report this species as shade tolerant and it is consistent with the characteristics given for this species by Quattrocchi (2006). Even though I found *P. conjugatum* in forested ecosystems it was rather rare. The other studies mentioned, were conducted in shaded crop sites, while this study was from shaded forest condition, and this difference could be the reason of the scarce presence of *P. conjugatum* in this study.

It was hypothesized that the distribution patterns of accompanying species would be a summary of the influence of all environmental variables in a plot. However, the characterization of plant assemblies with presence/absence of species was insufficient to distinguish clearly between plots. The cumulative variance of the DCA ordination axes was low, indicating high similarity among plots in terms of the composition of species (whether species occurred or not). However, some patterns are distinguishable. *P. conjugatum* seems more specialized environmental requirements than the other three target species. It was associated with species such *Eleusine indica*, *Desmodium* sp., *Crussea* sp and one undetermined grass. In contrast *P. notatum*, *P. virgatum* and *P. centrale* have more generalist environmental requirements and they do not have this association with their accompanying species.

Species basal cover and physiological performance

Some root and life history traits give to *P. notatum* and *P. conjugatum* advantages to perform better and cover more area than the other two target species. This is reflected in the total and average basal cover. *P. notatum* is a low growing, creeping plant, forming dense turfs, having short and stout rhizomes and stolons, and deep and extensive root system (Quattrocchi 2006). These traits allow it to adapt to a wide variety of soil water regimes and be a good competitor (Henry et al. 2009). This species may produce new ramets through the growth of persistent rhizomes and the production of numerous seeds (Henry et al. 2007). Similar traits allow to *Paspalum conjugatum* performing well in a wide variety of

environmental conditions. It is strongly stoloniferous (Quattrocchi 2006) with stolons up to three meters long (W3Tropicos 2012). These species has been widely reported as invasive and capable to form grass carpets, that makes difficult for other species to co-occur (Zanoni 2011, Acosta & Agüero 2012). The reproduction systems of these species also give them performance advantages through the clonal growth. *P. conjugatum* is considered very invasive in China, among the other reasons, due to its clonal growth (Liu 2006), and *P. notatum* has showed advantages in competition by clonal growth (Zanoni 2011). *P. centrale* and *P. virgatum* have not extended stolons, so they occur only as individual shoots or sometimes in dense clumps as in the case of *P. virgatum* but they never form carpets. The clonal growth in *P. virgatum* seems limited to form dense tussocks. *P. centrale* observed in field sampling seemed not have clonal growth and it was common to find single individuals.

In this study, *P. conjugatum* seems to be little more specialized than *P. notatum* and less competitive. Betlee (1974) states that *P. notatum* and *P. conjugatum* form part of different stages in the ecological succession process. In addition the presence of the highly competitive *Axonopus compressus* (Sw.) P. Beauv., in the Muy Muy region can be a barrier to the performance of *P. conjugatum*. *Axonopus compressus* is a very wide spread species and it was the most abundant everywhere, in all the habitats, topographic and vegetation cover conditions. *Paspalum notatum* as a better competitor than *P. conjugatum* can co-exist with *A. compressus*. In Muy Muy at middle altitude, in an area where normally *P. notatum* and *A. compressus* dominated, I found just one plot with presence of *P. conjugatum*, in this plot *P. notatum* and *A. compressus*

were not present. The competitive exclusion can be the reason why *P. conjugatum* is not appearing in the most humid soils, because it may have been excluded of clayish soils and wetter condition by *P. notatum* and *A. compressus*. In one lineal meter the size of the plants can be important too. *P. virgatum* is a robust species and when it is present could be difficult to others appear, although it happened some times. The co-occurrence of *P. notatum* and *P. notatum* at a segment of the 20 m lineal sampling happened only once. Cavender-Bares et al. (2006) suggest competitive exclusion should have greater importance at smaller spatial scales while environmental filtering should predominate at larger spatial scale.

The positive correlations between all the species and their fluorescence values can be interpreted as a good indicator that the abundance of the specimens means a good physiological performance of them.

Conclusion

The differences in the distribution of the four *Paspalum* target species at regional scale, appears to be influenced by land use. The agricultural practices and introduction of exotic grasses in Chacocente, and the constant agricultural rotations in Rivas seem to result in a decrease of grassland richness. The sampling in Chacocente was incomplete and sampling in seminatural grasslands inside the protected area is needed. The grasslands in Rivas and those sampled in Chacocente were homogeneous and dominated by the naturalized African grass *H. rufa*, and the presence of the target species was marginal; none in Chacocente and only two species in Rivas with very low abundances, *P. notatum* and *P. virgatum*. In contrast in Muy Muy, where the agriculture is limited and the use of sown pastures less extended, the presence *H. rufa* was marginal and the four *Paspalum* target species were present there.

At local scale the most important factor of variation were the soil and altitude. The distribution of three of the target species can be explained by these variables. *Paspalum notatum*, was negatively correlated with soil pH and silt content, and positively correlated with clay content. This species was the one with widest distributional range in the regions studied it was present on every topographic condition and in the majority of habitats types. This species seems to be limited locally by soil pH; it occurred in all soils types except those of higher pH. In this study, it was the most abundant of the target species.

Paspalum conjugatum was correlated with the topographical position mid slope, the position with the lowest levels of soil humidity. The literature is

reported that sometimes this species can support drought conditions (Beetle 1974). This species is positively correlated with altitude, soil pH, and soil silt content. It occurred preferentially at sampling sites with neutral soil pH. The limiting factors to the distribution of this species seem to be the altitude and clay soil content. It did not occur on clayish soils. *Paspalum conjugatum* was prone to occur at high altitudes and this places overlap with areas surrounded by forested ecosystems.

Paspalum centrale was associated with the habitat condition, charral and with the topographical condition mid slope. Soil humidity was negatively correlated with this species and it explained its preference to mid slope, the driest part of the topographic gradient. *Paspalum centrale* occurred in almost all the soil types but not in those with neutral soil pH and high phosphorous content, this species is negatively correlated with these parameters. *Paspalum centrale* occupied a wide distribution range in Muy Muy, but occurred with local low abundances. Its absence in the Rivas region leads to think that *P. centrale* is negatively affected by the disturbances.

Paspalum virgatum was not associated to any particular environmental variable. This finding could be interpreted as a generalist behavior and it explains the capacity of the species capacity to occur in a variety of conditions even in disturbed places.

Paspalum notatum and *P. centrale* were positively correlated. In turn, *P. notatum* and *P. virgatum* were negatively correlated.

The most abundant and extended of the target species was *P. notatum* followed by *P. conjugatum*. The first one forms extended and continuous

carpets. The second one appears only spread out in small patches. *Paspalum centrale* and *P. virgatum* had very scattered occurrences. They never form a continuous cover. In the case of *P. centrale*, it is common to find single individuals.

According to the literature, some traits such as root features and clonal growth, can give to *P. notatum* and *P. conjugatum* advantages to occupy more area over the other two target species. *Paspalum centrale* seems to have a limited clonal spread and in the case of *P. virgatum*, it forms tussocks.

The positive correlations between the basal cover of all the species and their fluorescence values can be interpreted as a good indicator that the abundance of the specimens reflects high physiological performance.

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Appendices

Appendix I. List of species

Species	Family	Habitat	Exotic/native
<i>Acacia cornigera</i> (L.) Willd.	Fabaceae	Shrub	N
<i>Acacia farnesiana</i> (L.) Willd	Fabaceae	Shrub	N
<i>Acalypha alopecuroidea</i> Jacq.	Euphorbiaceae	Herb	N
<i>Acalypha</i> sp.	Euphorbiaceae	Herb	N
<i>Acalypha</i> sp. 2	Euphorbiaceae	Herb	N
<i>Achyranthes aspera</i> L.	Amaranthaceae	Herb	E
<i>Aeschynomene americana</i> L.	Fabaceae	Herb	N
<i>Ageratum conyzoides</i> L.	Asteraceae	Herb	N
Amaranthaceae	Amaranthaceae	Tree	N
<i>Amaranthus spinosus</i> L.	Amaranthaceae	Herb	N
<i>Anacardium excelsum</i> (Bertero & Balb. ex Kunth) Skeels	Anacardiaceae	Tree	N
<i>Arachis pintoii</i> Krapov. & W.C. Greg	Fabaceae	Herb	E
Araceae 2	Araceae	Herb	N
Arbol rubiaceae	Rubiaceae	Tree	N
<i>Asclepias curassavica</i> L.	Asclepiadaceae	Herb	N
Asteraceae enredadera	Asteraceae	Herb	N
<i>Astrocaryum alatum</i> H.F. Loomis, J. Wash	Arecaceae	Tree	N
<i>Axonopus compressus</i> (Sw.) P. Beauv.	Poaceae	Herb	N
<i>Baltimora recta</i> L.	Asteraceae	Herb	N
Bambusoide	Poaceae	Herb	N
<i>Borreria prostrata</i> (Aubl.) Miq.	Rubiaceae	Herb	N
<i>Borreria remota</i> (Lam.) Bacigalupo & E.L. Cabral	Rubiaceae	Herb	N
<i>Urochloa decumbens</i> (Stapf) R.D. Webster	Poaceae	Herb	E
<i>Urochloa</i> sp.	Poaceae	Herb	E
<i>Bromelia</i> sp.	Bromeliaceae	Herb	N
<i>Bursera simaruba</i> (L.) Sarg.	Burseraceae	Tree	N
<i>Byrsonima crassifolia</i> (L.) Kunth	Malpigiaceae	Tree	N
<i>Byttneria aculeata</i> (Jacq.) Jacq.	Sterculiaceae	Shrub	N
<i>Calathea lutea</i> Schult.	Marantaceae	Shrub	N
<i>Calea urticifolia</i> (Mill.) DC.	Asteraceae	Herb	N
<i>Calycophyllum candidissimum</i> (Vahl) DC.	Rubiaceae	Tree	N
<i>Calopogonium mucunoides</i> Desv.	Fabaceae	Herb	N
<i>Caperonia pallustris</i> (L.) A. St.-Hil.	Euphorbiaceae	Herb	N
<i>Cassia grandis</i> L. f.	Fabaceae	Tree	N
<i>Cedrela odorata</i> L.	Meliaceae	Tree	N
<i>Centrosema</i> CF molle	Fabaceae	Herb	N
<i>Chamaecrista nictitans</i> (L.) Moench	Fabaceae	Herb	N
<i>Cissus verticillata</i> (L.) Nicolson & C.E. Jarvis	Vitaceae	Herb	N

Species	Family	Habitat	Exotic/native
<i>Coccocypselum hirsutum</i> Bartl. ex DC.	Rubiaceae	Herb	N
<i>Combretum fruticosum</i> (Loefl.) Stuntz	Combretaceae	Shrub	N
<i>Commelina diffusa</i> Burm	Commelinaceae	Herb	N
<i>Conostegia subcrustulata</i> (Beurl.) Triana	Melastomataceae	Shrub	N
<i>Cordia alliodora</i> (Ruiz & Pav.) Oken	Boraginaceae	Tree	N
<i>Cordia dentata</i> Poir.	Boraginaceae	Tree	N
<i>Croton argenteus</i> L.	Euphorbiaceae	Herb	N
<i>Croton lobatus</i> L.	Euphorbiaceae	Herb	N
Crusea 2	Rubiaceae	Herb	N
<i>Curatella americana</i> L.	Dilleniaceae	Tree	N
<i>Cynodon dactylon</i> (L.) Pers.	Poaceae	Herb	E
<i>Cynodon</i> sp.	Poaceae	Herb	E
<i>Cyperus digitatus</i> Roxb.	Cyperaceae	Herb	N
<i>Cyperus iria</i> L.	Cyperaceae	Herb	N
<i>Cyperus laxus</i> Lam.	Cyperaceae	Herb	N
<i>Cyperus luzulae</i> (L.) Rottb. ex Retz.	Cyperaceae	Herb	N
<i>Cyperus</i> sp.	Cyperaceae	Herb	N
<i>Cyperus rotundus</i> L.	Cyperaceae	Herb	E
<i>Cyperus tenerrimus</i> Presl & C. Presl in C. Presl	Cyperaceae	Herb	N
Desconocida		Herb	N
Desconocida total		Herb	N
<i>Desmodium distortum</i> (Aubl.) J.F. Macbr.	Fabaceae	Herb	N
<i>Desmodium procumbens</i> (Mill.) Hitchc. var. <i>Procumbens</i>	Fabaceae	Herb	N
<i>Desmodium</i> sp.	Fabaceae	Herb	N
<i>Desmodium triflorum</i> (L.) DC.	Fabaceae	Herb	N
<i>Dichanthium</i> CF. <i>Anulatum</i>	Poaceae	Herb	E
<i>Digitaria bicornis</i> (Lam.) Roem. & Schult.	Poaceae	Herb	N
<i>Dyschoriste quadrangularis</i> (Oerst.) Kuntze	Acanthaceae	Herb	N
<i>Echinochloa colona</i> (L.) Link	Poaceae	Herb	E
<i>Eclipta prostrata</i> (L.) L.	Asteraceae	Herb	N
<i>Eleocharis geniculata</i> (L.) Roem. & Schult.	Cyperaceae	Herb	N
<i>Eleusine indica</i> (L.) Gaertn.	Poaceae	Herb	E
<i>Enterolobium cyclocarpum</i> (Jacq.) Griseb.	Fabaceae	Tree	N
<i>Chamaesyce prostrata</i> (Aiton) Small	Euphorbiaceae	Herb	
<i>Euphorbia graminea</i> Jacq.	Euphorbiaceae	Herb	N
<i>Chamaesyce hirta</i> (L.) Millsp.	Fabaceae	Herb	E
Euphorbiaceae (foto José)	Euphorbiaceae	Herb	N
<i>Evolvulus nummularius</i> (L.) L.	Convolvulaceae	Herb	N
<i>Ficus</i> sp. (matapalo)	Moraceae	Tree	N
<i>Fimbristylis dichotoma</i> (L.) Vahl	Cyperaceae	Herb	N
<i>Gramma desconocida</i>	Poaceae	Herb	N
<i>Gronovia scandens</i>	Poaceae	Herb	N

Species	Family	Habitat	Exotic/native
Guazuma ulmifolia Lam.	Sterculiaceae	Tree	N
Guettarda macrosperma Donn. Sm.	Rubiaceae	Tree	N
Hamelia patens Jacq.	Rubiaceae	Shrub	N
Helicteres sp	Malvaceae	Shrub	N
Heliotropium indicum L.	Boraginaceae	Herb	N
Hymenaea courbaril L.	Fabaceae	Tree	N
Hymenocallis littoralis (Jacq.) Salisb	Amaryllidaceae	Herb	N
Hyparrhenia rufa (Nees) Stapf	Poaceae	Herb	E
Hyptis capitata Jacq.	Lamiaceae	Herb	N
Hyptis pectinata (L.) Poit.	Lamiaceae	Herb	N
Inga vera var. Vera	Fabaceae	Tree	N
Ipomea batatas (L.) Lam.,	Solanaceae	Herb	N
Ischaemum CF timorense	Poaceae	Herb	E
Kyllinga brevifolia Rottb.	Cyperaceae	Herb	N
Kyllinga pumila Michx.	Cyperaceae	Herb	N
Lantana camara L.	Verbenaceae	Shrub	E
Limonaria vellosa	Asteraceae	Herb	N
Lonchocarpus minimiflorus Donn. Sm.	Fabaceae	Tree	N
Ludwigia octovalvis (Jacq.) P.H. Raven	Onagraceae	Herb	N
Lygodium venustum Sw.	Schizaeacea	Herb	N
Malachra alceifolia Jacq.	Malvaceae	Herb	N
Malvaviscus arboreus Cav.	Malvaceae	Shrub	N
Maranta arundinacea L.	Marantaceae	Shrub	N
Myrsinaceae	Marantaceae	Shrub	N
Melochia sp	Malvaceae	Herb	N
Melochia tomentosa L.	Malvaceae	Herb	N
Mimosa albida Humb. & Bonpl. ex Willd.	Fabaceae	Shrub	N
Mimosa pigra L.	Fabaceae	Shrub	N
Mimosa pudica L.	Fabaceae	Shrub	N
Momordica charantia L.	Cucurbitaceae	Herb	E
Oplismenus burmannii var. nudicaulis (Vasey) McVaugh	Poaceae	Herb	N
Oxalis corniculata L.	Oxalidaceae	Herb	E
Pachira	Malvaceae	Tree	N
Palicourea sp.	Rubiaceae	Shrub	N
Steinchisma laxum (Sw.) Zuloaga	Poaceae	Herb	N
Panicum sp.	Poaceae	Herb	N
Passiflora sp.	Passifloraceae	Herb	N
Paspalum centrale Chase	Poaceae	Herb	N
Paspalum conjugatum P. J. Bergius	Poaceae	Herb	N
Paspalum costaricense Mez	Poaceae	Herb	N
Paspalum convexum Humb. & Bonpl. ex Flüggé	Poaceae	Herb	N
Paspalum CF. dilatatum	Poaceae	Herb	N

Species	Family	Habitat	Exotic/native
<i>Paspalum notatum</i> A. H. Liogier ex Flüggé	Poaceae	Herb	N
<i>Paspalum paniculatum</i> L.	Poaceae	Herb	N
<i>Paspalum virgatum</i> L.	Poaceae	Herb	N
<i>Phyllanthus caroliniensis</i> Walter ssp. <i>caroliniensis</i>	Euphorbiaceae	Herb	N
<i>Physalis angulata</i> L.	Solanaceae	Herb	N
<i>Pilea</i> sp.	Urticaceae	Herb	N
<i>Piper peltatum</i> L.	Piperaceae	Shrub	N
<i>Pithecellobium oblongum</i> Benth	Fabaceae	Tree	N
<i>Platymiscium dimorphandrum</i> Donn. Sm.	Fabaceae	Tree	N
<i>Polygala</i> sp.	Polygalaceae	Herb	N
<i>Portulaca oleracea</i> L.	Portulacaceae	Herb	
<i>Priva lappulaceae</i> (L.) Pers.	Verbenaceae	Herb	N
<i>Pseudoabutilon umbellatum</i> (L.) Fryxell	Malvaceae	Herb	N
<i>Pseudoelephantopus spicatus</i> (B. Juss. ex Aubl.) C.F. Baker	Asteraceae	Herb	N
<i>Psidium friedrichsthalianum</i> (O. Berg) Nied	Myrtaceae	Tree	N
<i>Psidium guajava</i> L.	Myrtaceae	Tree	N
<i>Psychotria</i> sp	Rubiaceae	Shrub	N
<i>Randia</i> sp.	Rubiaceae	Tree	N
<i>Raphanus raphanistrum</i> L	Brassicaceae	Herb	E
<i>Rhynchosia minima</i> (L.) DC.	Fabaceae	Herb	N
<i>Rhynchospora nervosa</i> (G. Mey.) T. Koyama	Cyperaceae	Herb	N
<i>Ricinus communis</i> L.	Euphorbiaceae	Shrub	E
<i>Rubiaceae</i> sp	Rubiaceae	Herb	N
<i>Ruellia blechum</i> L.	Acanthaceae	Herb	N
<i>Russelia sarmentosa</i> Jacq.	Scrophulariaceae	Herb	N
<i>Rytidostylis gracilis</i> Hook. & Arn.	Cucurbitaceae	Herb	N
<i>Stenorrhynchos lanceolatum</i> (Aubl.) Rich. ex Spreng.	Orchidaceae	Herb	N
<i>Samanea saman</i> (Jacq.) Merr.	Fabaceae	Tree	N
<i>Scleria melaleuca</i> Rchb. ex Schldl. & Cham.	Cyperaceae	Herb	N
<i>Scoparia dulcis</i> L.	Plantaginaceae	Herb	N
<i>Sellaginella</i>	Sellaginellaceae	Herb	N
<i>Senna obtusifolia</i> (L.) H.S. Irwin & Barneby	Fabaceae	Shrub	E
<i>Senna occidentalis</i> (L.) Link	Fabaceae	Shrub	N
<i>Senna skinneri</i> (Benth.) H.S. Irwin & Barneby	Fabaceae	Shrub	N
<i>Serjania atrolineata</i> C. Wrigth	Sapindaceae	Herb	N
<i>Setaria parviflora</i> (Poir.) Kerguélen	Poaceae	Herb	N
<i>Sida acuta</i> Burm. f.	Malvaceae	Herb	N
<i>Sida jussieuana</i> DC.	Malvaceae	Herb	N
<i>Sida linifolia</i> Cav.	Malvaceae	Herb	N
<i>Sida</i> sp.	Malvaceae	Herb	N
<i>Smilax spinosa</i> Mill.	Smilacaceae	Herb	N

Species	Family	Habitat	Exotic/native
<i>Solanum jamaicense</i> Mill.	Solanaceae	Shrub	N
<i>Spigelia</i> sp	Loganiaceae	Herb	N
<i>Spondias mombin</i> L.	Anarcadiaceae	Tree	N
<i>Sporobolus jacquemontii</i> Kunth	Poaceae	Herb	N
<i>Stachytarpheta frantzii</i> Pol	Verbenaceae	Herb	N
<i>Synedrella nodiflora</i> (L.) Gaertn.	Asteraceae	Herb	?
<i>Syngonium angustatum</i> Schott	Araceae	Herb	N
<i>Syngonium podophyllum</i> Schott	Araceae	Herb	N
<i>Tabebuia rosea</i> (L.) Gaertn.	Bignoniaceae	Tree	N
<i>Cascabela thevetia</i> (L.) Lippold	Apocynaceae	Tree	?
<i>Trichilia americana</i> (Sessé & Moc.) T.D. Penn.	Meliaceae	Tree	N
<i>Tridax procumbens</i> L.	Asteraceae	Herb	N
<i>Triunfeta lupulae</i> L.	Malvaceae	Shrub	N
<i>Tropeolaceae</i> sp.	Tropeolaceae	Herb	N
<i>Urera baccifera</i> (L.) Gaudich. ex Wedd.	Urticaceae	Shrub	N
<i>Urochloa fusca</i> (Sw.) B.F. Hansen & Wunderlin	Poaceae	Herb	N
<i>Vitex gaumerii</i> Greenm.	Verbenaceae	Tree	N
<i>Vitis</i> sp	Vitaceae	Herb	N
<i>Xanthosoma wendlandi</i> (Schott) Schott	Araceae	Herb	N
<i>Xylosma flexuosa</i> (Kunth) Hemsl.	Flacourtiaceae	Tree	N
<i>Zanthoxylum caribeum</i> Lam.	Rutaceae	Tree	N
<i>Zuelania guidonia</i> (Sw.) Britton & Millsp.	Flacourtiaceae	Tree	N

Appendix II. *Paspalum dilatatum* Poir



Appendix III. Results of soil analysis

Site	pHH ₂ O	pHKCl	C	N	P	CIC	soiltext	Sand	Limo	Clay
MY103	6,36	5,08	3,14	0,327	18,58	42,02	F-Arc	30,00	32,00	38,00
MY204	5,90	4,85	3,41	0,392	15,17	36,02	Arcillosa	26,00	30,00	44,00
MY305	6,04	4,66	2,76	0,333	15,72	29,09	F-Arc	36,00	32,00	32,00
MY701	5,97	4,66	3,29	0,350	12,99	23,43	Franca	38,00	36,00	26,00
MY802	6,38	5,14	3,60	0,378	49,97	30,40	Franca	34,00	40,00	26,00
MY903	6,53	5,69	4,41	0,697	47,06	37,57	F-Arc	27,00	35,00	38,00
MY1102	6,95	5,64	2,79	0,343	124,50	33,63	Franca	40,00	42,00	18,00
MY1203	6,61	5,34	3,34	0,347	39,01	31,31	Franca	34,00	40,00	26,00
MY1305	7,27	6,23	3,19	0,329	131,40	30,40	Franca	42,00	38,00	20,00
MY1601	4,49	5,08	2,97	0,322	50,38	24,44	Franca	38,00	40,00	22,00
MY1703	6,03	4,79	3,73	0,434	10,89	35,96	Franca	34,00	45,00	21,00
MY1804	6,34	4,94	3,16	0,385	11,71	42,28	Franca	36,00	40,00	24,00
MY1905	6,68	5,37	2,32	0,315	28,36	27,78	F-Arc	33,00	37,00	38,00
MY2201	6,50	5,07	2,55	0,242	13,76	51,51	F-Arc	28,00	34,00	38,00
MY2303	6,34	5,19	3,09	0,413	20,08	45,25	Arcillosa	26,00	32,00	42,00
RV303	6,71	5,04	1,68	0,154	44,65	34,14	Arcillosa	22,00	35,00	43,00
RV604	6,61	4,96	1,56	0,123	3,96	31,92	Arcillosa	14,00	21,00	65,00
RV905	7,12	6,02	2,25	0,354	54,07	31,71	F-Arc	34,00	34,00	32,00
RV1101	6,83	5,33	2,59	0,347	33,78	39,79	F-Arc- Li/F-Arc	20,00	42,00	38,00
RV1402	6,77	5,26	1,86	0,173	12,35	29,99	F-Arc/Arc	25,00	35,00	40,00